DEVELOPMENTAL STAGES IN THE LAGENIDÆ.

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THE Foraminifera present certain characters which make their study different from that of almost any other group of the animal kingdom. They are unicellular animals, but secrete a shell which in many cases has a considerable degree of complexity and shows marked stages in development. Their geological history is very long, for representatives are found in the Cambrian sedimentary rocks and more or less in intermediate horizons to the present time. At present, the Foraminifera are found, as a rule, in the deep waters of the oceans and extending toward the shores. Some twenty or more of the species occur as pelagic forms. In these animals the intermediate steps between extreme generic and specific forms are so well filled in, even in the living species, that some authors have regarded them all as simply variations of a single species. This is altogether too extreme a view. Intermediate species may be expected when the habits, environment, and reproductive characters of the animals are taken into consideration.

That the laws of development enunciated by Professor Alpheus Hyatt may be applied to this group, is shown in the following discussion. These laws have hitherto been applied only to groups of the Metazoa but as will be shown in the present paper they are equally applicable to another group of the animal kingdom, the Protozoa.

In tracing the development of Foraminifera where young individuals can be obtained, the relations are usually made out with ease. In the absence of young individuals the most reliable method is the study of sectioned specimens, since many species which are coiled, cover all traces of the younger portion externally by their later growth. Sectioning, in many cases, is the only method by which, from adults, the characters of the early growth may be seen in their true relations.

DEFINITION OF A FEW TERMS.

The following terms as defined, some of which are new, are convenient in the description of the structure of the shell of Foraminifera. The succeeding divisions of the shell are usually spoken of as chambers, the one first formed being the initial chamber (*I* in Figs. 1 and 2) and the last one built in any given specimen, the anterior chamber (*A*). The initial chamber which will be shown to have a decidedly phylogenetic bearing in the group is here given a distinctive name — the *proloculum*—to correspond with the term applied to the embryonic shell of other groups already worked out in the Metazoa. The ends of the shell as a whole are called anterior (*a*) and posterior (*p*). The walls of the chambers are called anterior and posterior walls according to their individual position in relation to the direction of growth. The line of contact made by the joining of a succeeding to a preceding chamber is called a suture (*S*). In coiled forms the outer border formed by the sum of the distal portion of the walls of succeeding chambers is called the peripheral margin. The angle between the suture and the distal wall of the next succeeding chamber in coiled forms is called the angle of curvature for that portion of the peripheral margin. These angles are shaded at *C*, *C'*, *C''*, to show the decided differences that the angle may assume.

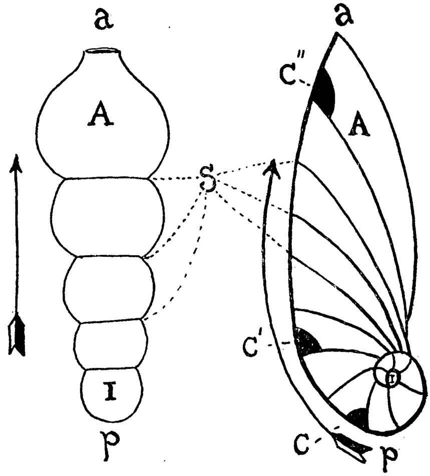

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FIG. 1.— Nodosaria. FIG. 2 — Uncoiled form of Cristellaria. *A*, anterior chamber; *I*, initial chamber or proloculum; *a*, anterior end; *p*, posterior end. Arrows show the direction of growth; shaded portions indicate the angle of curvature at *C*, *C*,' *C''*; *S*, sutures.

Development of Typical Species of Various Genera.

Lagena.— This genus represents the simplest condition seen in the family under discussion. In its geological history it can be traced from the Silurian to the present time. It is monothalamous or single-chambered (Fig. 3). The species very commonly develops a neck at the anterior end (Figs. 4, 5). The variation in forms of ornamentation is very remarkable and includes costæ, reticulate patterns, knobs, and bosses or broadly expanded wings of shelly material, but the underlying character of the chamber is always that of a simple flask-like form or a modification of it. This simple chamber represents the completed development of this genus, which is the only one of the family that has the single-chambered character. As it is the simplest form in the family and as all the other genera of the family start off with a simple chamber which is comparable to it, Lagena may be taken as the radical from which other genera of the family may be derived.

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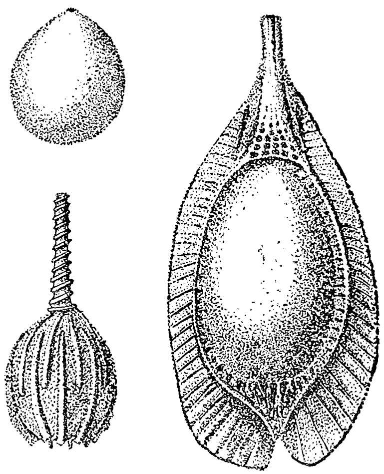

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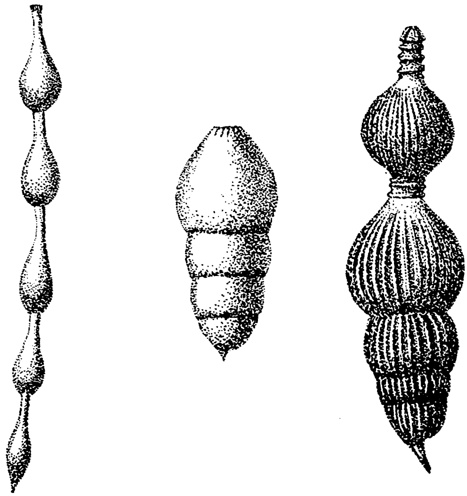
Figs. 3-5.— Three species of Lagena showing the great differences in ornamentation that are found in the group. Fig. 3, *Lagena globulosa* Montagu, a smooth type; Fig. 4, *L. sulcata* W. & J., var. *interrupta* Williamson, a costate type; Fig. 5, *L. formosa* Schwager, a type with expanded wing-like growths. (Figures after Brady.)

Nodosaria.— This genus in its typical form consists of a linear series of Lagena-like chambers, the posterior wall of each newly added chamber overlapping the anterior wall of the preceding one. The initial chamber or proloculum is comparable in character to the adult Lagena but the addition of the second chamber in Nodosaria shows that it is developing beyond the single-

chambered Lagena condition. The succeeding chambers add no striking characters in development further than that given by the second except in features of ornamentation which is a secondary character. The chambers of the linear series may be more or less closely overlapping (Figs. 6, 7) and this character



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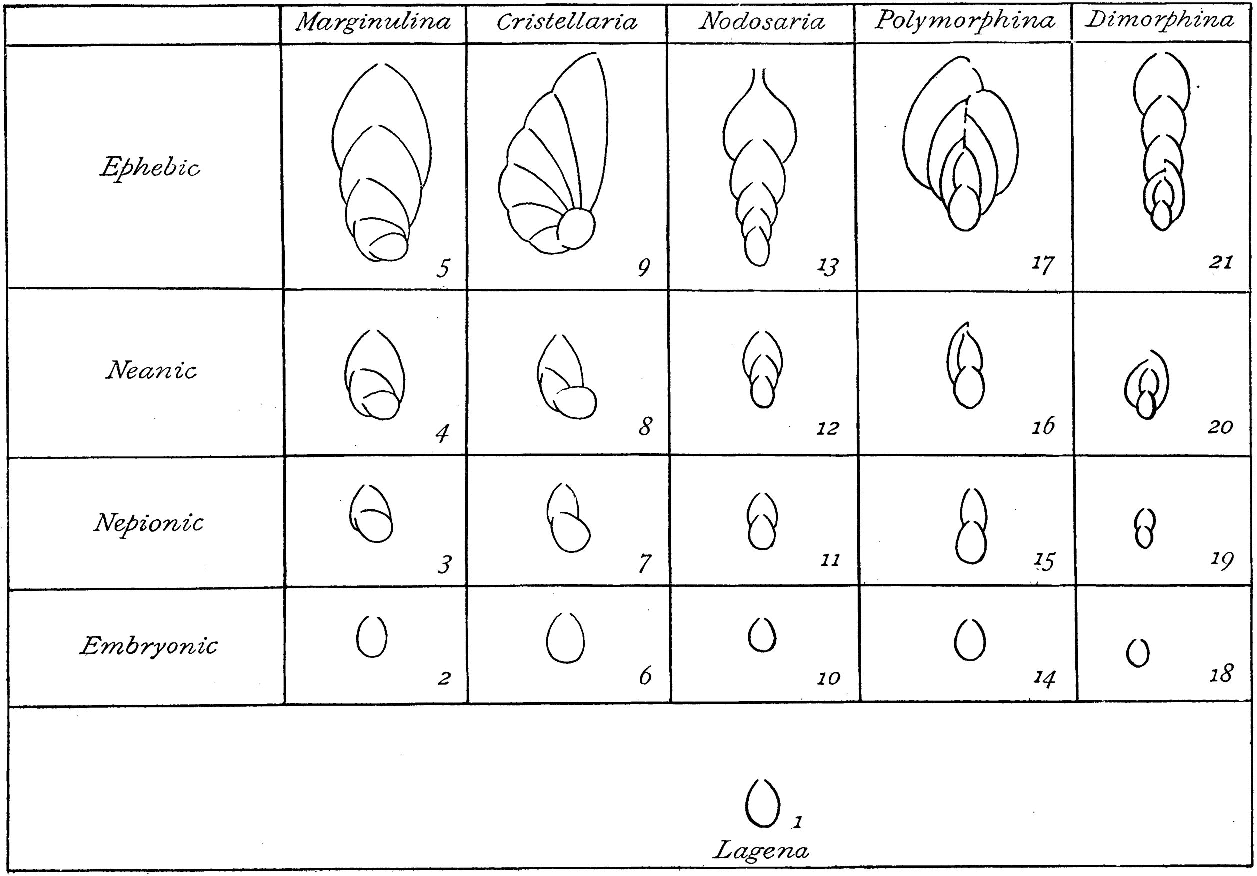
FIGS. 6–8.—Three species of Nodosaria showing the difference in the amount of overlapping, and in Fig. 8 the Lagena-like last chamber. Fig. 6, *Nodosaria pyrula* d'Orb.; Fig. 7, *N. radicula* Linn.; Fig. 8, *N. scalaris* Batsch (Figures after Brady.)

of overlapping may vary with the age of the individual as shown in progressively added chambers of *Nodosaria scalaris* var. *seperans* Brady (Fig. 8). They may also be variously ornamented according to the species but the linear series of chambers is always the essential character. Very often the last-formed or final chamber is more distinctly separated from the preceding ones and is decidedly Lagena-like (Fig. 8). Therefore at the end of growth representing old age or senescence, a chamber may occur which is closely comparable to the first stage of development in the young of the same individual or to the simpler genus Lagena. The stages of development of Nodosaria from young to old age may be expressed by a formula using the initial letters of the genera represented, as $L + N + L$.

Cristellaria.—The initial chamber or proloculum of Cristellaria, as in the other genera of the family, is simple and Lagena-like (Pl. 1, Fig. 6). The second chamber is added obliquely (Pl. 1, Fig. 7), as in some species of Nodosaria, and at this stage simply reveals the fact that it will not be a Lagena nor any of the straight Nodosarian forms. The third chamber of Cristellaria adds a decidedly new character. Instead of continuing on as in Nodosaria, it extends back on its inner margin so as to come in contact with the proloculum or initial chamber initiating the feature of coiling (Pl. 1, Fig. 8). In Cristellaria this coiled character is maintained throughout further growth in typical species as in Figs. 9, 18, 19. In further growth the shell may take on a flattened form as in *Cristellaria compressa* d'Orb., or may later take on a loose-coiled, or straight form of growth as in the species *C. siddalliana* Brady (Fig. 21) and *C. tenuis* Bornemann (Fig. 12) which are at present included in the genus. The typical Cristellaria is marked by the coiled form as the acme of its development (Figs. 18, 19), with a resulting close-coiled form throughout its life history beginning with the third nepionic chamber.

As with Nodosaria, a formula may be made to represent the stages in development. In Cristellaria it is the third chamber which is the determinative one, and the formula for the close-coiled form (Fig. 18) would be, Cristellaria = L + N + C. The absence of repetition of any letter in the formula indicates progressive development as a coiled form, as no senescence is seen in the form or arrangement of the chambers in typical species which are close coiled in the adult.

Cristellaria as at present recognized contains species showing excellent differences in the degree of acceleration of development. In such species as *C. articulata* Reuss (Fig. 9), the close-coiled character after being taken on, extends throughout the succeeding life history. In others, as *C. siddalliana* Brady (Fig. 10), the main part of the shell is close-coiled but towards the end of its growth there is an uncoiling seen in the last three chambers of this specimen. This is brought about by the failure of chamber 21 to extend back to the preceding coil and the continued shrinking away of the next-formed chambers, 22 and 23.


Marginulina
Cristellaria
Nodosaria
Polymorphina
Dimorphina
Ephebic
Neanic
Nepionic
Embryonic
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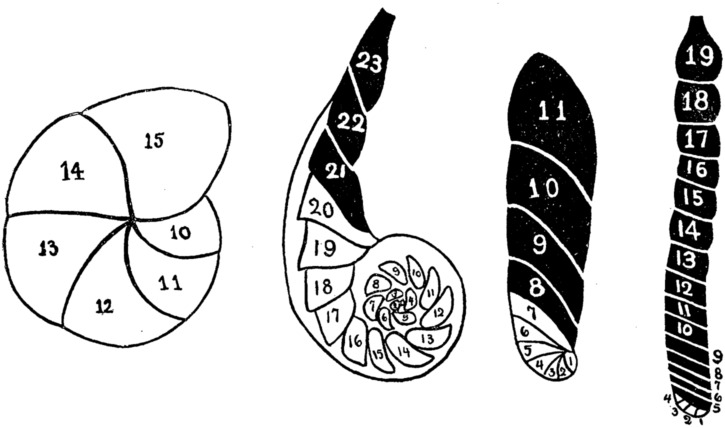
Lagena

PLATE 1.

The figures given show the ontogeny of representative genera of Lagenidæ, arranged to show comparative stages in development. 1, Lagena, the primitive radical; 2–5, stages in development of Marginulina; 6–9, Cristellaria; 10–13, Nodosaria; 14–17, Polymorphina; 18–21, Dimorphina; the embryonic stage, the proloculum, is represented in the lower row and may be compared to Lagena The nepionic, representing the first two chambers in the next row above, may be compared to Nodosaria. In the neanic shown in the third row the true generic characters are definitely taken on at least as regards progressive characters.

In uncoiling as is shown in Fig. 2, there is a decided change in the angle of curvature from an acute angle gradually to an obtuse one. This seems to be the rule in the stages by which a straight growth is produced from a coiled one as is shown again in Figs. 11 and 12. In *C. schlœnbachi* Reuss (Fig. 11), the uncoiled character is early taken on until on an average only the first six to eight chambers are coiled, while the succeeding chambers which constitute the major part of the whole growth, are



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FIGS. 9–12.— Four species of Cristellaria, showing different degrees in the acceleration of the character of uncoiling. Blackened chambers show the extent of the senescent uncoiled portion. Fig. 9, *Cristellaria articulata* Reuss; Fig. 10, *C. siddalliana* Brady; Fig. 11, *C. schlœnbachi* Reuss; Fig. 12, *C. tenuis* Bornemann. (Figures adapted from Brady.)

uncoiled. Thus the senescent character of uncoiling in this last species is more accelerated in its development than in *C. siddalliana* as it originates much earlier in the ontogeny or life history of the individual. In such a species as *C. tenuis* Bornemann (Fig. 12), the coiled portion is usually limited to the first four chambers, while the last fifteen or more are uncoiled. Other specimens of this species show fewer chambers than that figured. This species is then, even more accelerated in development, for the senescent character is so accelerated that it includes four fifths of the entire number of chambers. In the complete return to the straight Nodosarian growth, as shown in the last few chambers of this species, there is a return to a right

angle in the angle of curvature if it may be so called. In the entire development from the right-angled condition in the Nodosarian young, there is a change gradually to an acute, then a right, next an obtuse, and finally back to the right angle again. This then represents the mechanics of the uncoiling. The character of uncoiling in these four species of Cristellaria is represented in Figs. 9–12, in which the black chambers represent the portion showing senescent uncoiling. The white portion shows the extent of the coiled development.

Marginulina.— The first three chambers in the specimen of Marginulina figured (Pl. 1, Fig. 4), are exactly comparable to the same chambers of Cristellaria (Pl. 1, Fig. 8). The first chamber is Lagena-like, the addition of the second gives the oblique Nodosarian form, and the third is seen to be truly Cristellarian. The formula thus far would be as in the preceding, L + N + C. The fourth and fifth chambers in this specimen of Marginulina, however, present a new feature; they fail to extend back to the initial one, but strike off at a tangent showing the incipient stage of uncoiling. The chambers as built, continuing in the line or direction initiated by the fourth chamber, form a Nodosarian growth and the adult therefore may be represented by the formula, Marginulina = L + N + C + N. This is shown in Fig. 14 in section, and in Fig. 13 from the exterior.

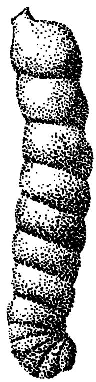

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FIG. 13.— *Marginulina ensis* Reuss, showing the main portion of the growth uncoiled.
FIG. 14.— Section through median line of *Marginulina glabra* d'Orb.

In certain cases in old age the last-formed chamber is less closely overlapping than the preceding and therefore takes on a form very much like Lagena. In Marginulina, representing this last chamber in the formula we have, Marginulina = L + N + C + N + L. This shows a complete cycle of stages seen in progressive and typical sen-

escent or regressive development. Such forms as that figured and the majority of species usually classed under Marginulina are not intermediate between Nodosaria and Cristellaria as is commonly stated, but are truly senescent species derived from Cristellaria and resulting from acceleration of development and the shoving back of the Cristellarian character to the early stages in development.

Polymorphina.—The proloculum or initial chamber in Polymorphina as shown in Fig. 15, is here also simple, like Lagena, as in the previous genera. The second chamber (Pl. 1, Fig. 15) is added in the same manner as in Nodosaria and in the second stage in all its visible characters Polymorphina apparently belongs to that genus. The addition of the third chamber (Pl. 1, Fig. 16) initiates a new character in the line of development. It continues back over the preceding one to the proloculum as in Cristellaria but is added in a different manner being so placed that the aperture faces the line of the median axis. This generic character may be represented by P and the formula for the genus may be expressed as follows: Polymorphina = L + N + P. The fourth chamber also extends back to the initial chamber (Pl. 1, Fig. 17) but is added on the opposite side from the third with its aperture facing and occluding that of the third, and this character continues throughout further growth to the adult. This is then a progressive form and after its Nodosarian second stage, starts a new line of development which at once places it in a different group from Cristellaria and Marginulina.

FIG. 15.—Section through median plane of *Polymorphina compressa* d'Orb. After Flint.

Dimorphina.— In this genus the early stages up to the fourth chamber (Pl. 1, Fig. 20,) are exactly as in Polymorphina and may be represented by the same formula, L + N + P. If the animal had died at this stage it would be described as Polymorphina. After this stage, however, a quite different mode of growth is assumed. Beginning with the fifth chamber, suc-

ceeding chambers are arranged in a linear series and are therefore Nodosarian in character. The formula for the adult would be, Dimorphina $= L + N + P + N$. The last chamber is often more or less free and like Lagena. The formula for the completed growth including this gerontic character will then be, Dimorphina $= L + N + P + N + L$. Dimorphina is therefore a senescent genus having as its basis the three progressive characters of Polymorphina and in senescence has, by retracing in inverse order, attained in the last chamber to a condition comparable to that seen in the proloculum, or in other words to Lagena. Having completed the cycle, such forms evidently have attained completion along certain lines of development and no new forms can originate from this senescent type except in regard to minor changes in character of ornamentation which are recognized as specific and not generic in value.

Senescent Characters.

Characters showing typical senescence are frequent among the Foraminifera and illustrate in simple terms conditions similar to those found in many other groups of the animal kingdom. The simplest of these senescent characters is the loss of ornamentation. The ornamentation of this group is shown mainly by elevated ridges, by tubercles, or by spines. Examples of the loss of these will be given. As found by Hyatt in Cephalopoda, the uncoiling of forms, which in their early development were close-coiled, is a decided feature of senescence. Such cases are seen in their simplest terms among the Foraminifera. As shown by Beecher, one of the characters apt to appear in the decline of a group is a peculiar spinose or extravagant growth, "wild" growth, as it is sometimes called in the Foraminifera. Certain senescent genera of Foraminifera show this character exceptionally well. One of the surest indications of senescence is a return to the simpler conditions seen in the young of the same individual and in the adults of more primitive forms. Excellent and at the same time very simple cases of this are seen in Dimorphina and in Dentalinopsis. The Foraminifera as uni-

cellular organisms seem to present the simplest conditions and examples for the expression of the various laws of development that can be found anywhere in the animal kingdom.

Loss of Ornamentation.

Ridges.—In a specimen of *Uvigerina angulosa* Williamson, var. *spinipes* Brady (Fig. 16), the early chambers have definite raised costæ or ridges running generally parallel to the axis of the growth of the shell. In later growth this character becomes less pronounced and in the last five chambers which by measurement represent more than half of the growth, is entirely wanting, and the chambers are perfectly smooth. Although not included in this family, *Bulimina subornata* Brady is figured here for comparison. It shows in much the same manner (Fig. 17) the costate early growth and the gradual disappearance and final loss of costation in the old age of the individual.

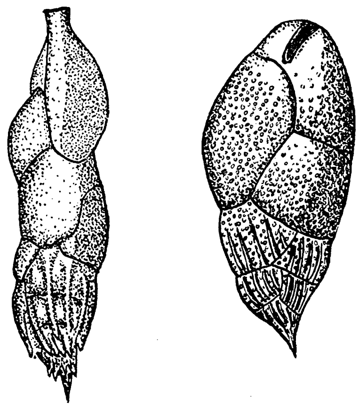

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Fig. 16.—*Uvigerina angulosa* Williamson, var. *spinipes* Brady, showing loss of ornamentation in senescence.

Fig. 17.—*Bulimina subornata* Brady, showing similar senescence. (After Brady.)

Tubercles.—In *Cristellaria echinata* d'Orb. (Fig. 18), the early growth is marked by rows of bead-like tubercles over the sutures, while the intermediate space is covered with hemispherical granules. In later growth these scattered granules are limited to the peripheral portion and on the last two chambers are entirely wanting, so that the surface of these chambers is smooth. The rows of bead-like tubercles also disappear in old age and pass into a smooth ridge. Similar conditions are found in various groups of the Mollusca, especially in certain of the fossil Trigonias. In such forms the costæ break up into knobs and bosses in development, and later in the old age of

the individual again resume a costate condition by the merging together of the tubercles.

Spines. — In the preceding species, *C. echinata* d'Orb. (Fig. 18), the loss of spines is a very evident character in senescence.

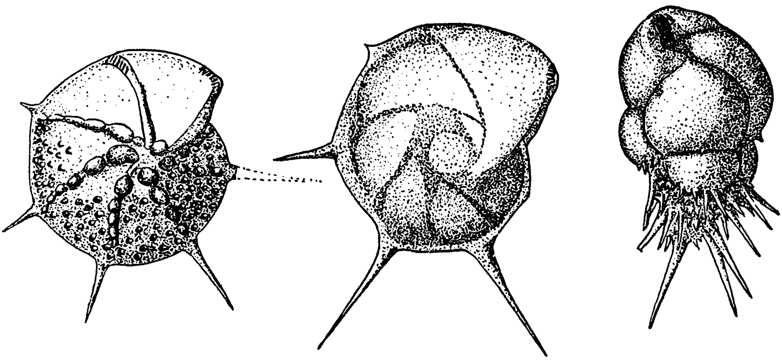

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FIG. 18 — *Cristellaria echinata* d'Orb., showing loss of ornamentation in senescence.
FIG. 19.— *C. calcar* Linn., showing loss of spines.
FIG. 20 — *Bulimina aculeata* d'Orb., showing similar loss of spines (After Brady.)

In the median portion of growth the peripheral spines at the sutures are long, at least equalling the length of the chamber on the peripheral margin. The third from the last is shorter and the last two spines decrease progressively in size, the last one being very short, while at the last suture no spine at all is developed. Much the same condition of affairs in regard to the reduction and loss of spines is seen in *C. calcar* Linn. (Fig. 19), in which, however, the spines do not coincide with the suture lines. Another excellent example, although not in the same family, is that presented by *Bulimina aculeata* d'Orb. (Fig. 20). Here the early growth is marked by well developed spines. As growth progresses, the spines of successively added chambers are not so greatly developed. Toward the later growth, traces of them are seen in the very reduced spines at the posterior angles and on the last-formed chambers they are lacking, and the chambers are perfectly smooth.

These examples of loss of ornamentation as a character in senescence are exactly comparable to cases already worked out

by others in the Cephalopoda, Pelecypoda, Gastropoda, and Brachiopoda and they are seen in still other groups.

Uncoiling.— *Cristellaria siddalliana* Brady (Fig. 21) shows an excellent case of uncoiling not carried to an extreme. The

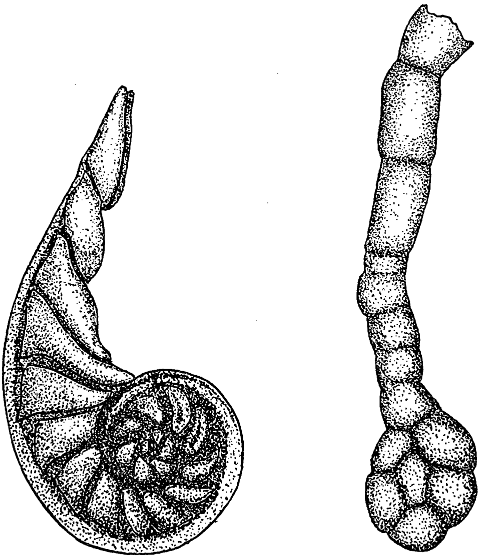

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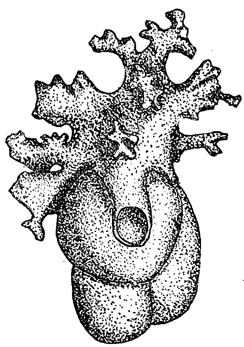
FIG. 21.— *Cristellaria siddalliana* Brady, showing uncoiling in last few chambers.
FIG. 22.— *Trochammina lituiformis* Brady, showing uncoiling carried to an extreme.

early chambers are close-coiled and this feature continues until the last few chambers. Here there is a distinct change and an uncoiled form is produced as shown in the figure. This uncoiling is only seen in well advanced specimens that show old age characters. Other examples of uncoiling in Cristellaria have already been given (Figs. 11, 12). Although outside of this family, *Trochammina lituiformis* Brady is figured (Fig. 22) to show the character of uncoiling carried to an extreme. The early chambers make a little more than a single volution, while the succeeding growth is uncoiled. In old age specimens, this character may be carried to a greater extent than is shown in Fig. 22. In this species in contrast to the preceding, the majority of the chambers form the uncoiled portion of the shell. Such examples are exactly comparable to Baculites or Lituites

among the Cephalopoda or to Vermetus or Magilus among the Gastropoda.

Spinose or "Wild" Growths.— In Polymorphina and Sagrina of this family the last chambers are often peculiarly different from the preceding ones. In *Polymorphina orbignyii*, as figured by Brady, Parker, and Jones (*Trans. Linn. Soc. London*, vol. 27, p. 244, pl. 42, fig. 38c) the last chamber is marked by a peculiar fistulose growth, greatly differing from the preceding regular chambers of the species (Fig. 23). Such growths are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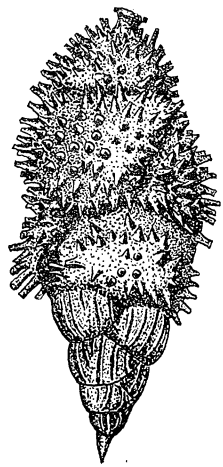
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FIG. 23.— *Polymorphina orbignyii* with peculiar fistulose growth in senescence.
FIG. 24.— *Uvigerina aculeata* d'Orb. with "wild" growth. (After Brady.)

not infrequent in various other genera. Corresponding "wild" growths appear in certain species of Cristellaria. In *Uvigerina aculeata* d'Orb. (Fig. 24) similar characters appear. This species in its younger development has simple longitudinal costæ. Later, however, there is a thickening by addition from the outside and the last chamber is covered with a decidedly spinose development totally different from the previous ornamentation. This spinosity may continue, extending progressively posteriorly until it envelops the whole shell, covers the preceding chambers, and hides all traces of the typical earlier ornamentation. These growths seem to be best regarded as senescent charac-

ters. Such a decided change in method of growth, with an increase in the thickness of the shell without corresponding increase in the number of chambers, may be compared in a general way to the building up of tissue in the old age of Brachiopoda and Mollusca where there is no increase in size of the living chamber but frequently a decrease. It may be more closely compared to similar conditions which appear in the Gastropoda for example in the several Eocene species of Calyptraphorus where by reflection of the mantle in later growth a callous develops which hides the previous sculpturing.

RETURN TO SIMPLER CONDITIONS.

Dimorphina.— In this genus, the development of which has already been noted, there is a return to a straight uniserial growth in the later chambers. This was expressed by the formula L+N+P+N+L. It is a true return to the Nodosarian and Lagena characters seen in the progressive development of the first two chambers. The biserial Polymorphine character in Dimorphina is accelerated so that it may appear in but two chambers including the third and fourth and a return to the uniserial condition is then taken on in the fifth. This return to the simpler Nodosarian condition, seen in the young of the same individual and again as the acme of development in an ancestral type, Nodosaria, can be regarded only as a truly senescent character and the genus Dimorphina a senescent one derived from Polymorphina.

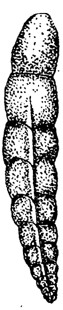

FIG. 25.— *Dentalinopsis subtriquetra* Reuss, showing return to circular cross section in the last-formed chamber. (After Reuss.)

Dentalinopsis.— In this genus (Fig. 25), the early chambers are uniserial like those of Nodosaria. At first they are circular in cross section but soon become triangular or polygonal. At this point the species which have this character as their highest development are classed under the genus Rhabdogonium which is characterized by angular section in the adult. The formula for Rhabdogonium would be L + N + R.

Senescent forms have been found among the fossils and to such forms Reuss has applied the generic name Dentalinopsis. In species of this genus the later growth instead of being triangular reverts to its earlier circular cross section and becomes truly Nodosarian. Reuss noted the generic value of this senescent character, although his genus has not always been recognized by later writers. The last-formed chamber may be more free and distinctly Lagena-like, thus completing the reversion in senescence. The formula for a specimen which has the Lagena-like last chamber would be $L + N + R + N + L$, showing its definite regressive senescence.